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辽宁北票尾羽龙(*Caudipteryx*)一新种[1)]

周忠和[1] 汪筱林[1,2]

(1 中国科学院古脊椎动物与古人类研究所 北京 100044)

(2 中国地质大学地球科学与资源学院 北京 100083)

1998年夏,中国科学院古脊椎动物与古人类研究所辽西野外考察队在北票上园张家沟采集到一块保存相当完整的、属于尾羽龙的头后骨架。该材料被订立一新种,对尾羽龙的已知特征作了重要的补充和修订。本文是对这一新材料的初步记述,并简单讨论了尾羽龙的系统位置和习性。

尾羽龙科(新科)Caudipteridae fam. nov.

尾羽龙属 *Caudipteryx* Ji *et al.* 1998

董氏尾羽龙(新种)*Caudipteryx dongi* sp. nov.

(图 1～3; 图版 I～V)

词源 种名谨献给我国杰出的恐龙学家董枝明先生(注:"*Caudipteryx*"被一些作者译为"尾羽鸟",笔者认为这不符合原作者和国际上多数学者对这一化石隶属恐龙的看法)。

正型标本 一件近完整的头后骨架。中国科学院古脊椎动物与古人类研究所标本编号V 12344。

产地与层位 辽宁省北票市上园乡四合屯村张家沟;义县组(早白垩世)。

特征 胸骨小,股骨与胸骨长比率约6.0(邹氏尾羽龙为4.1)。第一掌骨与第二掌骨长比率约0.45(邹氏尾羽龙为0.40)。坐骨较短。肠骨较长。

对尾羽龙特征的补充 董氏尾羽龙(*Caudipteryx dongi* sp. nov.)的发现使尾羽龙的许多重要特征得以补充和修订,它们包括:肋骨发育钩状突;耻骨伸向下前方,这和Ji *et al.*(1998)所推测的尾羽龙具有与鸟类和驰龙相似的后转型腰带的结论相反;腓骨长,在远端和跟骨相接;第一趾与其他三趾对握,为和鸟类相似特征,这一特征尚未可靠出现在其他恐龙中;在四个脚趾骨中,第三趾最长,第二趾次之,第一趾最短;远端趾节比近端趾节明显缩短,为快速奔跑动物共有之特征;初级飞羽最长超过股骨,但尚未发育羽小枝;前肢尚未发育小翼羽。

讨论 尾羽龙最初被描述为带羽毛的恐龙(Ji *et al.*, 1998)。这一观点得到国际上大多数学者的赞同,但同时还有一些学者对此有不同看法,他们认为 *Caudipteryx* 可能是次

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1) 中国科学院资源与生态环境研究"九五"重大项目(编号:KZ951-B1-410)、中国科学院创新工程重大项目(编号:KZCX3-J-03)、国家自然科学基金重点项目(编号:49832002)和中国科学院"百人计划"资助。

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生失去飞翔能力的鸟类。他们列举的鸟类特征包括：真正的羽毛，牙齿基部收缩，尾巴缩短。除此以外，新种还保存了另外一些和鸟类相似的特征，如第一脚趾和其他三趾形成对握，肋骨上发育和鸟类十分相似的钩状突起，肠骨上的 M. cuppedicus 肌窝退化等。尽管如此，在总体骨骼形态上尾羽龙和手盗龙类（Maniraptora Gauthier 1986）十分接近，而和鸟类存在显著的区别。这些原始特征包括：1）颧骨较短并具较高的背突；2）尾椎的脉弧较始祖鸟发育；3）肩胛骨远端膨大，鸟类肩胛骨远端尖细；4）肩胛骨和乌喙骨的夹角显著大于 90°；5）一对胸骨片未愈合成一个完整的胸骨；6）第一、二掌骨长的比率大于始祖鸟和孔子鸟；7）第一指的第一指节远端伸达第二指第一指节的中部；8）肠骨的耻骨突位置不如鸟类向后伸展；9）坐骨保留大的闭突；10）耻骨伸向下前方，腰带为蜥臀类恐龙典型的三叉型，不同于所有已知鸟类；11）耻骨联合长超过耻骨总长的一半，而在始祖鸟和孔子鸟中约为三分之一；12）跟骨和距骨不和胫骨愈合；13）前胫骨（pretibial）缺失；14）第三蹠骨在中间明显侧扁；15）跗蹠骨未愈合，16）前肢远短于后肢。

我们认为，尾羽龙具有的鸟类特征，有些在其他的恐龙中也已有报道，如窃蛋龙便具有和尾羽龙十分相似的肋骨的钩状突（Clark *et al.*, 1999），肠骨上退化的 M. cuppedicus 肌窝也见于一些窃蛋龙类，牙齿基部的收缩见于驰龙等多种恐龙（徐星，pers. comm.）。如果假设尾羽龙为次生失去飞翔能力的鸟类，那么，我们就必须承认，以上所列举的所有原始特征都是次生演化的结果，其中包括耻骨由后转重新回到前转的位置，鸟类特有的前胫骨退化消失等等。 基于以上分析，我们认为尾羽龙更可能是带羽毛的恐龙而非次生失去飞行的古鸟。当然今后更进一步的工作也许会得出不同的结论。

尾羽龙最初被认为是和鸟类关系最接近的一类恐龙（Ji *et al.*, 1998），这一观点随后便受到种种挑战。目前颇具代表性的一种看法是，尾羽龙和窃蛋龙的关系最近（Sereno, 1999）。尾羽龙在腰带、肋骨的钩状突，以及头骨的特征上确实和窃蛋龙比较相近，但在另外一些方面也和驰龙等相似。此外，尾羽龙还具有许多特有的特征，如第三蹠骨在中间显著侧扁，坐骨的闭突特别发育，第一趾与其他趾形成对握，第四趾骨较第二趾骨短，尾椎少而短等。鉴于此，本文建议建立一新科，尾羽龙科（Caudipteridae fam. nov.），代表一不同于已知手盗龙类主要类群的新的演化支系。手盗龙类是 Gauthier （1986）创立的分类单元，下属于恐龙纲（Dinosauria Owen 1842）中的兽脚亚目（Theropoda Marsh 1881）。所有的现生及化石鸟类也被他归入到手盗龙类。

尾羽龙的牙齿大多退化，具有胃石，颈椎较多，这些特征都表明它是一类食植物性的动物。尾羽龙的第二趾爪不像驰龙那样特别发育，前肢的指爪相对较小，加之前肢有羽毛的附着，不可能是凶猛的动物。尾羽龙的前肢特别缩短，可能和它的捕食功能的退化有关。特别加长的后肢，侧向缩窄的蹠骨、退化缩短的第一趾、第四趾的相对减短，以及前后趾节的比例等还表明，尾羽龙是一类快速奔跑的动物。不论在系统关系上究竟多近，在总的生活习性和食性方面，在已知的恐龙中，尾羽龙和窃蛋龙可能是最为相似的。

关键词 辽宁北票，早白垩世，尾羽龙

中图法分类号 Q915.864

A NEW SPECIES OF *CAUDIPTERYX* FROM THE YIXIAN FORMATION OF LIAONING, NORTHEAST CHINA

ZHOU Zhong-He[1] WANG Xiao-Lin[1,2]

(1 *Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences* Beijing 100044)

(2 *College of Earth Science and Resources, China University of Geosciences* Beijing 100083)

Abstract A recently collected specimen of *Caudipteryx* is described as a new species: *C. dongi* sp. nov. Compared with the type species of *Caudipteryx* (*C. zoui*) the new species has relatively long iliums and smaller sternal plates. Uncinate processes are present as in oviraptorids and most birds. The pubis is antero-ventrally directed as in most saurischian dinosaurs. The fibula contacts the calcaneum distally. Among the pedal digits the third is the longest, the fourth is shorter than the second, and the hallux is short with a reduced claw characteristic of cursorial animals. As in birds the hallux is opposable to the rest of digits, indicating that the ancestor of *Caudipteryx* might have obtained perching or grasping power, therefore providing further evidence for the arboreal hypothesis of the origin of avian flight. The feather lacks barbules and represents either a more primitive type than in birds or a secondarily reduced one. Although *Caudipteryx* has several bird characters it is interpreted in this paper as a feathered dinosaur rather than a secondarily flightless bird. *Caudipteryx* resembles oviraptorids more than dromaeosaurids, yet it represents a lineage distinguishable from all known major maniraptorian clades, therefore we propose to erect a new family: Caudipteridae fam. nov. currently including only *Caudipteryx*. The characters of *Caudipteryx* also indicates that it was a fast running herbivorous animal.

Key words Liaoning, Early Cretaceous, *Caudipteryx*

1 Introduction

Caudipteryx was first reported and briefly described by Ji *et al.* (1998) as a feathered dinosaur based on two nearly complete and partially articulated skeletons with feather impressions on the forelimb, tail and body. *Caudipteryx* was regarded as a maniraptorian that is closer to birds than to other known dinosaurs by Ji *et al.* (1998). This feathered creature has stimulated a lot of discussions and controversies ever since its publication. Many workers have compared it with oviraporids while others considered it as a flightless bird (Feduccia, 1999; L. D. Martin, T. Jones, pers. comm.).

In the summer of 1998, a nearly complete postcranial skeleton of *Caudipteryx* was collected by the field crew of the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences. The specimen was from the Yixian Formation at the Zhangjiagou Locality which is about 3 kilometers northeast of the famous Sihetun Locality in Beipiao, Liaoning Province of northeast China (Wang *et al.*, 1998, 1999). The new material represents a large individual and a new species of the genus *Caudipteryx*. The wing feathers were well-preserved. The postcranial skeleton was better preserved and more articulated than the two known specimens of *Caudipteryx zoui*. The new species preserved a lot more new information about the morphology of *Caudipteryx* and provides more evidence for understanding the systematic position and habit of this important feathered creature.

2 Systematics

Dinosauria Owen 1842

Theropoda Marsh 1881

Maniraptora Gauthier 1986

Caudipteridae fam. nov.

***Caudipteryx* Ji *et al.* 1998**

***Caudipteryx dongi* sp. nov.**

(figs. 1~3; pls. I~V)

Etymology '*dongi*' refers to Zhiming Dong, a distinguished Chinese dinosaur expert.

Holotype An incomplete individual with nearly complete forelimbs, hindlimbs and pelves. Institute of Vertebrate Paleontology and Paleoanthropology, V 12344.

Locality and horizon Zhangjiagou, Sihetun, Beipiao, Liaoning Province, northeast China; Layer 6 of Yixian Formation (Early Cretaceous).

Diagnosis Sternum small, femur to sternum ratio, 6.0 (4.1 in *C. zoui*). Metacarpal I to Metacarpal II ratio, 0.45 (0.40 in *C. zoui*). Ischium short. Ilium long.

Description The skull was not preserved. There is an isolated bone near the ribs, which is tentatively recognized as the pterygoid. It is fan-shaped and expanded dorsally. Another separate bone near the first caudal vertebra is probably the frontal (fig. 1; pl.I). The vertebral column was not completely preserved. Vertebrae are mostly disarticulated. The cervical vertebra bears short and slender ribs. It appears to be amphicoelous. The dorsal vertebra lacks noticeable pleurocoels; the neural spine is low and wide; the centrum is procoelous. The unfused sacral vertebrae are wide with the transverse processes strongly expanded distally. The anterior 11 caudal vertebrae were well-preserved and mostly articulated; among the haemal spines, the first is the

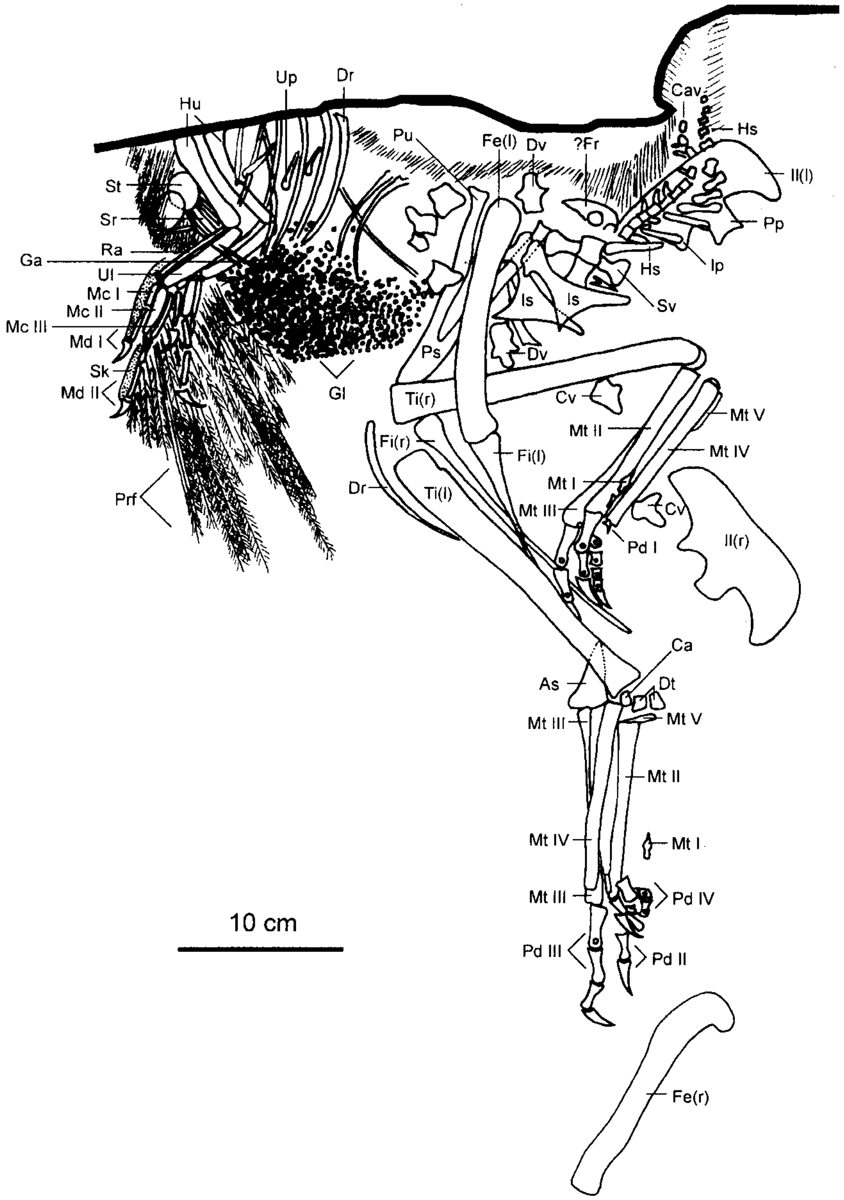


Fig. 1 Holotype of *Caudipteryx dongi* sp. nov. (IVPP V 12344)

简字说明 Abbreviations: As, astragalus 距骨; Ca, calcaneum 跟骨; Cav, caudal vertebra 尾椎; Cv, cervical vertebra 颈椎; Dr, dorsal rib 背肋; Dt, distal tarsal 远端跗骨; Dv, dorsal vertebra 背椎; Fe(l), left femur 左侧股骨; Fe(r), right femur 右侧股骨; Fi(l), left fibula 左侧腓骨; Fi(r), right fibula 右侧腓骨; ?Fr, ?frontal ?额骨; Ga, gastralia 腹肋; Gl, gastroliths 胃石; Hs, haemal spine 脉弧; Hu, humerus 肱骨; Il(l), left ilium 左侧肠骨; Il(r), right ilium 右侧肠骨; Ip, ischiadic peduncle 坐骨突; Is, ischium 坐骨; Mc I–III, metacarpals I–III 第 1–3 掌骨; Md 1–2, manual digits 1–2 第 1–2 指骨; Mt I–V, metatarsals I–V 第 1–5 蹠骨; Pd I–IV, pedal digits I–IV 第 1–4 脚趾骨; Prf, primary feathers 初级飞羽; Pp, pubic peduncle 耻骨突; Ps, pubic symphysis 耻骨联合; Pu, pubis 耻骨; Ra, radius 桡骨; Sk, skin impression 皮肤印痕; Sr, sternal rib 胸肋; St, sternum 胸骨; Sv, sacral vertebra 荐椎; Ti(l), left tibia 左侧胫骨; Ti(r), right tibia 右侧胫骨; Ul, ulna, 尺骨; Up, uncinate process 钩状突

longest and rod–shaped, it tapers towards the distal end; the second to fourth haemal spines are slightly shorter; the haemal spine of the fifth caudal is only about half the length of the first; the rest of the haemal spines are expanded at both ends and decrease in length posteriorly. The caudal vertebrae are not fused. The transverse processes of the caudal also decrease in length posteriorly (pl.III).

The sternum is composed of two unfused sternal plates. The sternal plate is flat and lacks a keel; it is about 2.5 cm long and 2.0 cm wide. The sternum lacks costal processes that are present in *Sinornithosaurus* (Xu *et al.*, 1999) and most birds. Sternal ribs were preserved associated with the sternum, they are straight, slightly longer than the sternum and flatter than the dorsal ribs. Several pairs of crossing gastralia were well preserved in front of the gastroliths (gizzard stones); they are short, curved and much slender than the dorsal and sternal ribs. Three uncinate processes are present, ranging from 2 to 3 cm in length; they are flat, slightly curved and expanded at the ventral ends; they articulate with the dorsal ribs at about the middle position. The gastroliths are more or less rounded pebbles and range from 0.2 to 0.9 cm in length, but most of them are 0.3～0.4 cm long.

The coracoid was incompletely preserved. It is short and has a convex ventral margin and a concave posterior margin. Like *Archaeopteryx* and most theropods it also has a well–developed biceps tubercle (Ostrom, 1976).

The forelimbs are nearly complete (fig. 1; pl.II). The proximal end of the humerus is missing. The deltoid crest of the humerus is moderately developed; it is less expanded than that of *Confuciusornis*. The humerus is longer than the ulna and radius as in *Archaeopteryx*, *Confuciusornis* and theropod dinosaurs. The ulna is bow–shaped, the radius is relatively straight. The preserved angle between the manus and the forearm is much larger than 90 degrees while in most birds including *Archaeopteryx* and *Confuciusornis*, the angle is close to or lower than 90 degrees.

The manus is longer than the ulna as in *Archaeopteryx* (Wellnhofer, 1993) and *Confuciusornis* (Zhou and Hou, 1998; Martin *et al.*, 1998); In more advanced birds such as *Cathayornis*, the manus is shorter than the ulna (Zhou *et al.*, 1992). The carpals are not fused with the metacarpals; there is an isolated carpal near the distal end of the radius, it is square–shaped and probably the radiale. The second (major) metacarpal is as long as but about twice as wide as the third (minor) metacarpal; the ratio of the first (alular) metacarpal to the second metacarpal is about 0.45. In *Archaeopteryx* and *Confuciusornis* the first metacarpal is only about one third of the length of the second. The proximal end of the third metacarpal is slightly laterally compressed and appressed to the proximal second metacarpal.

The first digit is long; its first phalanx extends distally to the middle of the first phalanx of the second digit; the ungual is large and curved, but is shorter than the

first phalanx. The second digit is the longest among the three digits; the second phalanx is much longer than the first, the ungual is as long as the ungual of the first digit. The third digit is not fully prepared out so as to preserve the feather impressions; from the exposed part, it shows that the third digit is much more slender than the other two digits; the third digit also crosses the second digit as in birds and a few theropod dinosaurs, an indication of attachment of primary feathers (Zhou and Martin, 1999).

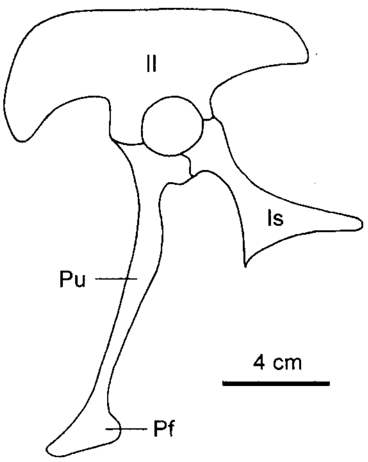


Fig.2 Reconstruction of the pelvis of *Caudipteryx*, left side in lateral view
简字说明 Abbreviations: Il, ilium 肠骨; Is, ischium 坐骨; Pf, pubic foot 耻骨的脚状突; Pu, pubis 耻骨

The pelvic elements were well-preserved and unfused (fig. 2; pls. I, III). As in dromaeosaurs the preacetabular portion of the ilium is as long as the postacetabular portion; in early birds the preacetabular portion is longer than the postacetabular one. The ilium has a deep preacetabular portion that tapers ventro-anteriorly and extends as ventrally as the pubic peduncle. The postacetabulur portion tapers posteriorly as in *Deinonychus* and other dromaeosaurs and early birds, but is less pointed at the posterior end. The ilium also lacks a large and deep iliac fossa for M. cuppedicus that is large and deep in *Deinonychus* and other dromaeosaurs (Norell and Makovicky, 1997) but reduced or lost in oviraptorids (pers. observ.) and early birds (Chiappe, 1996). The acetabulum is large, the ratio of the acetabulum to ilium length is about 0.21 (0.11 in *Confuciusornis*). The pubic peduncle is much deeper than the ischiadic peduncle as in dromaeosaurs and birds; in oviraptorids the pubic peduncle is nearly as deep as the ischiadic peduncle. The pubic peduncle forms the anterior wall of the acetabulum; in birds the pubic peduncle extends further ventrally and posteriorly, therefore, it forms the anterior part of the ventral wall of the acetabulum. The pubic peduncle has a large ventral notch as in dromaeosaurs, but in lateral view the pubic peduncle has a flat ventral margin compared to a concave margin in dromaeosaurs and convex margin in oviraptorids (pers. observ.).

The ischium has a triangular shaft that bears a large and pointed obturate process; it is more robust than in dromaeosaurs, oviraptorids and birds. The pubis is antero-ventrally oriented as in oviraptorids and most saurischian dinosaurs but is different from that of dromaeosaurs, segnosaurids (Barsbold, 1983) and birds. The pubis is long and nearly twice the length of the ischium; it has a short pubic foot.

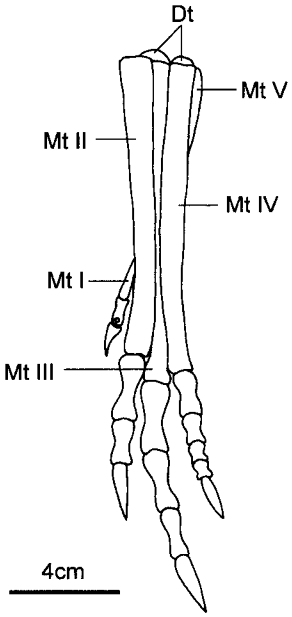


Fig. 3 Reconstruction of the hindlimb of *Caudipteryx*, left side in dorsal view
简字说明 Abbreviations: Dt, distal tarsal 远端跗骨; Mt I–V metatarsals I–V 第 I–V 蹠骨

The pubic symphysis is about half the length of the pubis; in *Archaeopteryx* and *Confuciusornis* it is only about one third of the length of the pubis; in more advanced birds such as *Cathayornis* the pubic symphysis is further shortened.

The hindlimbs were completely preserved and well articulated (fig. 3; pls. I, IV). The femur is moderately curved. The right femur is shorter than the left femur, which is probably an abnormal feature of this individual. The large head is well separated from the greater trochanter. The greater trochanter is slightly lower than the head. The fibula is as long as the tibia; it tapers distally for the proximal third length and remains constantly slender, flat, and rod–shaped throughout the rest of the length. It should be in touch with the calcaneum distally. The astragalus is unfused with the tibia. The ascending process of the astragalus is about 20.5% the length of the tibia. The calcaneum is a separate disk–like bone. There appear to exist two distal tarsals that are positioned on the three major metatarsals (II–IV) although mostly on metatarsals III and IV.

The three main metatarsals (II–IV) are not fused (fig. 3). Among the five metatarsals the third is the longest, the second is slightly shorter than the fourth. The second metatarsal is as wide as the fourth metatarsal. The mid–shaft of the third metatarsal is, however, laterally compressed and appears much narrower than the second and fourth metatarsals in cranio–posterior view. Proximally the third metatarsal participates in the articulation with the distal tarsals. The fifth metatarsal is slender and rod–shaped, it is about 29% the length of the third metatarsal, which is similar to that of *Confuciusornis* while in *Archaeopteryx* (Wellnhofer, 1993) the fifth metatarsal is relatively shorter (about one fourth of the tarsometatarsus).

The proximal end of the first metatarsal is positioned about one third of the way up the second metatarsal from the distal end. It is articulated with the postero–medial side of the second metatarsal. It is different from the usually "J"–shaped first metatarsal in birds. It is symmetric and has pointed proximal end; the distal half is constricted with a well–developed ball–shaped articulating end for the first phalanx.

The first phalanx of the first digit is shorter than all the phalanges of the second

and third digits; distally it does not extend to the distal end of the second metatarsal as in oviraptorids (Clark *et al.*, 1999) and *Deinonychus* (Ostrom, 1990) while in another dromaeosaur (Norell and Makovicky, 1997) it extends past the distal end of the second metatarsal distally, and in birds it extends even further distally. The first digit appears to be reversed as compared to the rest of the digits. The first phalanx of the first digit is about 90 degrees turned from the position of other digits. In oviraptorids (Clark *et al.*, 1999) and dromaeosaurs (Norell and Makovicky, 1997) the position of the first phalanx of the first digit is, however, similar to that of other digits. The ungual of the first digit is much shorter and less curved than the rest of the pedal unguals, and it is reversed compared to other unguals.

Among the four pedal digits the third is the longest, it is about two thirds of the length of the third metatarsal. The first phalanx is the longest as typical of theropods and many birds. The second phalanx is shorter and the third phalanx is the shortest among the phalanges of the third digit. The ungual is curved; it is about as long as the third phalanx, and is slightly longer than the ungual of the fourth digit. The second pedal digit is as robust as the third but is much shorter; the first phalanx is nearly as long as that of the third digit, it is much longer than the second phalanx as typical of cursorial animals; the ungual is curved and longer than the second phalanx. The fourth digit is shorter than the second digit; the first phalanx is nearly as long as the ungual and is much longer than the second and the third; the fourth phalanx is the shortest among the phalanges of the fourth digit. In *Deinonychus*, troodontids, *Archaeopteryx* and *Confuciusornis* (Hou *et al.*, 1995; Martin *et al.*, 1998), the fourth pedal digit is longer than the second digit.

The feathers are nearly distributed across the whole body of the skeleton (fig. 1; pls. I, V). The primary feathers were well preserved although the exact number of the primary feathers are hard to determine. They are attached to the second metacarpal, the first phalanx and all the way to the tip of the second phalanx of the second manual digit. The feather has a distinct rachis and vane. The primary feathers are slender and generally become shorter toward the distal end. Barbs of adjacent feathers overlap. There is no evidence of barbules on the barbs. The longest primary feather is about 182 mm long, which is longer than the femur; the vanes appear to be symmetric as in flightless birds. The secondary flight feathers were less well preserved; they are shorter than the primary feathers. The tip of the tail was unfortunately not preserved; short tail feathers were preserved along the ventral margin of the caudals from the 10th caudal to about 20th caudal, they average about 25 mm in length. The body feathers along the pectoral region were also well preserved.

It is noteworthy that the skin impression was well preserved along the distal forearm and the manual digits (fig. 1; pl. II). The skin doubles the width of the digits

when the animal was alive. The first digit lacks the alula that has been reported in enantiornithines (Sanz *et al.*, 1996; Hou *et al.*, 1999) but still unknown in *Archaeopteryx* and *Confuciusornis* (Zhou and Hou, 1998).

Measurements (mm) of the holotype of *Caudipteryx dongi* (V 12344; * indicates estimated measurement)

Maximum dorsal rib length	100*	Femur length (left)	152
Maximum sternal rib length	35	Femur length (right)	146
Maximum uncinate process length	30	Femur mid-shaft width	17
Sternal plate length	25	Tibia length	196
Humerus length	73*	Fibula length	181
Humerus mid-shaft width	9	Metatarsal I length	19
Ulna length	61	Metatarsal II length	112
Ulna mid-shaft width	5	Metatarsal III length	124
Radius length	58*	Metatarsal IV length	116
Radius mid-shaft width	4	Metatarsal V length	36*
Manus length	90.5	First phalanx of pedal digit I length	12
Metacarpal I length	13	Second phalanx of pedal digit I length	11
Metacarpal I proximal end width	6	First phalanx of pedal digit II length	25
Metacarpal II length	29	Second phalanx of pedal digit II length	16
Metacarpal II proximal end width	5.5	Third phalanx of pedal digit II length	19
Metacarpal III length	27	First phalanx of pedal digit III length	27
Metacarpal III proximal end width	3.5	Second phalanx of pedal digit III length	20
First phalanx of manual digit I length	25	Third phalanx of pedal digit III length	17
Second phalanx of manual digit I length	15	Fourth phalanx of pedal digit III length	20
First phalanx of manual digit II length	18.5	First phalanx of pedal digit IV length	15
Second phalanx of manual digit II length	25	Second phalanx of pedal digit IV length	9
Third phalanx of manual digit II length	18	Third phalanx of pedal digit IV length	7
Ilium length	115	Fourth phalanx of pedal digit IV length	7
Ilium height	54	Fifth phalanx of pedal digit IV length	16
Ischium length	73	Maximum length of primary feather	182
Leg total length	55.3		

3 Discussion

3.1 Comparison with *Caudipteryx zoui* and revised characters of *Caudipteryx*

The holotype of *Caudipteryx dongi* is a large individual. The average length of the leg is 553 mm, and the two known specimens of *C. zoui* are 550 and 540 mm long respectively (Ji *et al.*, 1998). The length of the tibia of *C. dongi* is 196 mm, which is larger than that of the two published *C. zoui* specimens (188 and 182 mm respectively). The ilium is 115 mm long in *C. dongi* and 101 mm in *C. zoui*. *C. dongi* can be well distinguished from *C. zoui* by a smaller sternum. The sternum is 25 mm long in *C. dongi* and 36 mm in *C. zoui*. A recently collected yet uncatalogued specimen referable to *C. zoui* is smaller than the holotype of *C. dongi* and its sternum is longer than 30 mm. The ischium of *C. dongi* is about 73 mm long while the ischium of *C. zoui* is 77 mm long. The ratio of metacarpal I to II length is 0.45 in *C.*

dongi and only about 0.4 in *C. zoui*. Therefore, *C. dongi* appears to be slightly more primitive than *C. zoui* in having a relatively long metacarpal I and a short sternum.

The deep pubic peduncle has a notch in the ventral margin in both *C. zoui* and *C. dongi*. Ji *et al.* (1998) interpreted this feature as characteristic of opisthopubic pelves; however, the holotype of *C. dongi* clearly shows that the pubis is antero-ventrally directed as in oviraporids and most saurischian dinosaurs but not in dromaeosaurs and birds. The pubic peduncle has a flat ventral margin in lateral view, which is different from the concave margin in dromaeosaurs and convex margin in oviraptorids. The fibula was not completely preserved in the specimens of *C. zoui*, it was fortunately completely preserved in *C. dongi*. The fibula is only slightly shorter than the tibia, and it should be in touch with the calcaneum as in oviraptorids and most theropods. The fifth metatarsal was not reported in *C. zoui*; it was, however, well-preserved in *C. dongi*; it is a slender rod-like bone as in *Deinonychus*, oviraptorids, *Archaeopteryx* and *Confuciusornis*.

The uncinate process was not preserved in *C. zoui* (fig. 1; pl.II); however, in *C. dongi* at least three uncinate processes were recognized, they articulate with dorsal ribs near the mid-shaft. In shape they generally resemble those of oviraptorids (Clark *et al.*, 1999) and early ornithurine bird *Chaoyangia*(Hou and Zhang, 1993).

C. dongi also preserved completely articulated pedal digits that were largely unknown in *C. zoui*. The third digit is the longest and the fourth is shorter than the second. The hallux is reversed as in birds but the ungual is shorter than the unguals of other digits. The reversed hallux may indicate that the ancestors of *Caudipteryx* had obtained perching or grasping capability (fig. 1; pl. IV), supposedly a prerequisite for the origin of avian flight, therefore supporting the arboreal hypothesis of the origin of avian flight.

The remiges were well preserved in *C. dongi*, the length of the longest primary feather is longer than the femur (fig. 1; pl. I). In *C. zoui*, the remiges were not completely preserved and the longest preserved remiges is shorter than the femur. The barbules are not observable in the feathers, they had probably not yet developed in *Caudipteryx*, therefore the feather in *Caudipteryx* is probably more primitive than that of birds. An alternative explanation is that it is secondarily reduced.

3.2 Feathered dinosaur or flightless bird?

Caudipteryx was described as a feathered dinosaur that provides the first evidence of real feathers in dinosaurs (Ji *et al.*, 1998). This opinion, however, has been challenged by many paleornithologists who suggest that *Caudipteryx* was probably a flightless bird, a "Mesozoic kiwi"(Feduccia, 1999; Martin, Jones, pers. comm.). The new material preserved some information that may shed new light on the discussion of the dinosaurian or avian state of this feathered creature.

Caudipteryx preserved several bird characters that are usually absent in dinosaurs. For instance, the hallux is reversed in the foot as in birds but not in dinosaurs; the iliac fossa for M. cuppedicus, a depression in the ventral portion of the preacetabular wing of the ilium, is large and deep in *Deinonychus* and other dromaesaurs (Norell and Makovicky, 1997) but is absent or reduced in *Caudipteryx* as in *Archaeopteryx* and *Confuciusornis*; the uncinate process of the ribs is absent in most theropods and early birds, but is present in *Caudipteryx*, oviraptorids and advanced birds such as *Chaoyangia* (Hou and Zhang, 1993); the teeth of *Caudipteryx* are constricted at the base of the crown as typical of all toothed birds and a few dinosaurs (X. Xu, pers. comm.); the tail is about as long as the tibia and is relatively shorter than that of *Archaeopteryx*.

On the other hand, *Caudipteryx* preserved many more characters that are similar to those of maniraptorian dinosaurs and are more primitive than in birds. They include: 1) the jugal is short with a high dorsal ascending process; 2) the haemal spines are more developed than in *Archaeopteryx* (Wellnhofer, 1974); 3) the scapula is expanded at the distal end; 4) the angle between the scapula and the coracoid is much larger than 90 degrees; 5) the sternal plates are unfused; 6) the ratio of metacarpal I to II length is about 0.45 and only about 0.36 in *Confuciusornis* and 0.33 in *Archaeopteryx*; 7) the first phalanx of the first manual digit extends distally to the middle of the first phalanx of the second manual digit; 8) the pubic peduncle does not extend posteriorly to below the middle of the acetabulum; 9) the obturate process of the ischium is large; 10) the pubis is antero-ventrally directed as in most saurischian dinosaurs but not dromaeosaurids and birds; 11) the pubic symphysis is at least half the length of the pubis while in *Archaeopteryx* and *Confuciusornis* it is close to or less than one third the length of the pubis, in more advanced birds the pubic symphysis is further reduced; 12) the astragalus and calcaneum are separated from the tibia; 13) the pretibial bone is present in birds (Martin *et al.*, 1980) but is absent in *Caudipteryx*; 14) the mid-shaft of the third metatarsal is laterally compressed; 15) the tarsometatarsus is unfused; and 16) the forelimb is much shorter than the hindlimb.

To argue for the avian state of *Caudipteryx* would require all aforementioned sixteen and more characters to be reversed from its presumed bird ancestors including the propubic pelvis reversed from the ancestral opithopubic pelvis. However, if *Caudipteryx* is interpreted as a feathered theropod dinosaur, the few bird characters can be explained either by parallel evolution or by their appearance before the origin of birds. Parsimoniously we believe the later scenario is more likely because over the past years many of the previously held bird characters such as the furcula and opithopubic pelvis have now been proved to be present in many theropod dinosaurs (Sereno, 1999). And the constriction at the base of the teeth has been reported in

several theropods including dromaeosaurs (X. Xu, pers. comm.).

Admittedly, even modern flightless birds resemble small theropods in many respects including the fused scapula and coracoid with an angle larger than 90 degrees, reduction of the furcula, and loss of the asymmetric flight feathers, therefore it would be easy to understand the difficulty to distinguish a small theropod with avian appearance from a primitive flightless bird of the Early Cretaceous. Neotenic characters in primitive flightless birds could have been easily interpreted as primitive characters in phylogenetic analysis. Therefore, although *Caudipteryx* is interpreted as a feathered dinosaur in this paper, we believe that the debate on the dinosaurian or avian state of *Caudipteryx* and oviraptorids (Elzanowski, 1999) will continue.

3.3 Comparisons with oviraptorids, dromaeosaurids and other maniraptorians

Caudipteryx was regarded as the closest relative of birds by its original workers (Ji *et al.* 1998); this view, however, has been challenged by many dinosaurologists who generally associated it with oviraptorids (Sereno, 1999).

Caudipteryx has a shortened first metacarpal which is less than half the length of the second metacarpal as in dromaeosaurids, troodontids and birds. The fused furcula has been discovered in oviraptorids (Norell *et al.*, 1997), dromaeosaurids (Burnham and Zhou, 1999; Xu *et al.*, 1999) and birds.

The pelvis of *Caudipteryx* is generally more similar to oviraptorids than to dromaeosaurs in having a footed pubis that is antero–ventrally directed; it also has a reduced iliac fossa for M. cuppedicus as in oviraptorids and birds but a large and deep one in dromaeosaurs.

Caudipteryx also shares with oviraptorids uncinate processes, loss of teeth and a short and high skull. At least three uncinate processes are present but not fused with the ribs in both groups. Uncinate processes have not been discovered in dromaeosaurids.

As in dromaeosaurs the first digit of the forelimb of *Caudipteryx* is not as robust as in oviraptorids. The pubic peduncle is much deeper than the ischiadic peduncle as in dromaeosaurs and birds; in oviraptorids the pubic peduncle is nearly as deep as the ischiadic peduncle.

Caudipteryx also has many distinctive characters that prevent it from being referred to either Oviraptorosauria or Dromaeosauridae. For instance, the tail has fewer than 25 caudals and is shorter than all known oviraptorids and dromaeosaurids. The ischium of *Caudipteryx* has an extremely large triangular obturator process that is less developed in both dromaeosaurids and oviraptorids. The mid–shaft of the third metatarsal is significantly medio–laterally compressed; in oviraptorids and *Sinornithosaurus* (X. Xu, pers. comm.), the third metatarsal only narrows slightly at the proximal end; in theropods such as many ornithomimids (Barsbold and Osmólska,

1990), elmisaurids (Currie, 1990), troodontids (Osmólska and Barsbold, 1990) the third metatarsal tapers proximally; in most birds and some dromaeosaurs (Norell and Makovicky, 1997) the width of the third metatarsal does not change much from the proximal to the distal end (Chiappe, 1996). The fourth digit is shorter than the second digit. The hallux of the foot is reversed in *Caudipteryx*, which is different from other known theropods (Norell and Makovicky, 1997; Clark *et al.*, 1999).

In summary, dromaeosaurids are probably the closest relatives of birds (Padian and Chiappe, 1998; Xu *et al.*, 1999; Sereno, 1999). Both *Caudipteryx* and oviraptorids are too specialized to be ancestral to birds (for instance, the large leg to arm ratio and the medio–laterally compressed third metatarsal) although they independently developed some bird characters such as the uncinate process and the reduction of teeth. Furthermore, *Caudipteryx* also has some features that are more similar to dromaeosaurs and birds than to oviraptorids, it could be the sister group of Oviraptorosauria or a separate lineage somewhere between Oviraptorosauria and Dromaeosauridae. Based on the peculiar combination of characters in *Caudipteryx* we propose to erect a new family: Caudipteridae fam. nov. currently including only *Caudipteryx*.

3.4 Diet and habits of *Caudipteryx*

The maxilla and the dentary are edentulous in *Caudipteryx*. The gastroliths were well preserved. The gastroliths have not been reported in carnivorous dinosaurs except in a recently discovered ornithomimid dinosaur (Yoshitsugu *et al.*, 1999). The jaws are edentulous in most ornithomimids. The long neck is composed of at least ten cervical vertebrae in *Caudipteryx*. A recently discovered herbivorous oviraptorid has 13 cervical vertebrae (J. Lü, pers. comm.). These characters suggest a herbivorous diet of *Caudipteryx* similar to that of ornithomimids and oviraptorids.

The ungual of the second pedal digit is relatively wide, but not elongated, there is no "killing claw" as in *Deinonychus* (Ostrom, 1969; 1990) and troodontids. The unguals of the forelimbs are relatively small and the attachment of long wing feathers to the arm prevents it from being predatory.

The ratio of the hindlimb to the forelimb is higher than in other coelurosaurs (Ji *et al.*, 1998) except alvarezsaurids (Perle *et al.*, 1994), the forelimb of which was probably specialized for a certain way of digging as in fossorial mammals (Zhou, 1995). The extreme shortening of the forelimb in *Caudipteryx* is probably a reflection of the reduction of the use of the forelimb. In *Caudipteryx* the long wing feathers were most likely used in display.

In the foot of *Caudipteryx*, the first phalanx of the hallux does not extend to the distal end of the second metatarsal which is similar to the situation in *Deinonychus*; in another dromaeosaur it extends distally past the distal end of the second metatarsal

(Norell and Makovicky, 1997); in birds it extends even further distally. This character, together with the high position of the articulation between the hallux and the second metatarsal, the relatively short and less curved ungual of the hallux, indicates that *Caudipteryx* is a good cursorial animal. The opposable hallux was interpreted here as a retained character of their ancestors with perching or grasping habit.

The fourth digit is shorter than the second digit, which may be another piece of evidence for specialized terrestrial life. In arboreal *Archaeopteryx* and *Confuciusornis*, the fourth pedal digit is longer than the second digit. The phalangeal proportions of the foot of *Caudipteryx* are also characteristic of fast cursorial animals with the proximal phalanges much longer than the second and/or third phalanges in the second and third digits.

The shortened tail, the compact metatarsals and the lightly built body are also consistent with the general conclusion about the habit of *Caudipteryx*, i. e., a fast, cursorial herbivorous animal.

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References

Barsbold R, 1983. Carnivorous dinosaurs from the Late Cretaceous of Mongolia. Joint Soviet-Mongolian Palaeontol Exped Trans, **19**: 1～119

Barsbold R, Osmólska H, 1990. Ornithomimosauria. In: Weishampel D B, Dodson P, Osmólska H eds. The Dinosauria. Berkeley: California Univ Press. 225～244

Burnham D, Zhou Z, 1999. Comparing the furcula in birds and dinosaurs. J Vert Paleont, **19**(suppl to no.3): 34A

Chiappe L M, 1992. Enantiornithine (Aves) tarsometatarsi and the avian affinities of the Late Cretaceous Avisauridae. J Vert Paleont, **12**(3): 344～350

Chiappe L M, 1996. Late Cretaceous birds of Southern South America: anatomy and systematics of Enantiornithes and *Patagopteryx deferrariisi*. Münchner Geowiss Abh (A), **30**: 203～244

Clark J M, Norell M A, Makovicky P, 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. Am Mus Novit, (3265): 1～36

Currie P J, 1990. Elmisauridae. In: Weishampel D B, Dodson P, Osmólska H eds. The Dinosauria. Berkeley:

California Univ Press. 245～248

Elzanowski A, 1999. A comparison of the jaw skeleton in theropods and birds, with a description of the palate in the Oviraptoridae. Smithson Contrib Paleobiol, **89**:311～323

Feduccia A. 1999. The origin and evolution of birds (2nd edition). New Haven: Yale University Press. 1～466

Gauthier J, 1986. Saurischian monophyly and the origin of birds. Mem California Acad Sci, **8**:1～55

Hou L H(侯连海), Zhang J Y(张江永), 1993. A new fossil bird from Lower Cretaceous of China. Vert PalAsiat(古脊椎动物学报), **31**(3):217～224 (in Chinese with English summary)

Hou L, Zhou Z, Martin L D *et al.*, 1995. A beaked bird from the Jurassic of China. Nature, **377**:616～618

Hou L H(侯连海), Martin L D, Zhou Z H(周忠和) *et al.*, 1999. *Archaeopteryx* to opposite birds-missing link from the Mesozoic of China. Vert PalAsiat(古脊椎动物学报), **37**(2):88～95

Ji Q, Currie P, Norell M A *et al.*, 1998. Two feathered dinosaurs from northeastern China. Nature, **393**:753～761

Martin L D, Stewart J D, Whetstone K N, 1980. The origin of birds: structure of the tarsus and the teeth. The Auk, **97**:86～93

Martin L D, Zhou Z, Hou L *et al.*, 1998. *Confuciusornis sanctus* compared to *Archaeopteryx lithographica*. Naturwissenschaften, **85**:286～289

Norell M A, Makovicky P, 1997. Important features of the dromaeosaur skeleoton; information from a new specimen. Am Mus Novit, (3215):1～28

Norell M A, Makovicky P, Clark J M, 1997. A *Velociraptor* wishbone. Nature, **389**:447

Osmólska H, Barsbold R, 1990. Troodontidae. In: Weishampel D B, Dodson P, Osmólska H eds. The Dinosauria. Berkeley: California Univ Press. 259～268

Ostrom J H, 1969. Osteology of *Deinonychus antirrhopus*, an unusual theopod from the Lower Cretaceous of Montana. Peabody Mus Nat Hist Yale Univ Bull, **30**:1～165

Ostrom J H, 1976. *Archaeopteryx* and the origin of birds. Biol J Linn Soc, **8**:91～182

Ostrom J H, 1990. Dromaeosauridae. In: Weishampel D B, Dodson P, Osmólska H eds. The Dinosauria. Berkeley: California Univ Press. 269～279

Padian K, Chiappe L M, 1998. The origin and early evolution of birds. Biol Rev, **73**:1～42

Perle A, Chiappe L M, Barsbold R *et al.*, 1994. Skeletal morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of mongolia. Am Mus Novit, (3105):1～29

Sanz J L, Chiappe L M, Perez-Moreno B P *et al.*, 1996. An Early Cretaceous bird from Spain and its implications for the evolution of avian flight. Nature, **382**:442～445

Sereno C P, 1999. The evolution of dinosaurs. Science, **284**:2137～2147

Wang X L(汪筱林), Wang Y Q(王元青), Wang Y(王原) *et al.*, 1998. Stratigraphic sequence and vertebrate-bearing beds of the lower part of the Yixian Formation in Sihetun and neighboring area, western Liaoning, China. Vert PalAsiat(古脊椎动物学报), **36**(2):81～101 (in Chinese with English summary)

Wang X L(汪筱林), Wang Y Q(王元青), Jin F(金帆) *et al.*, 1999. The Sihetun fossil vertebrate assemblage and its Geological setting in western Liaoning, China. Palaeoworld, **11**:240～257 (in Chinese with English summary)

Wellnhofer P, 1974. Das fünfte Skelettexemplar von *Archaeopteryx*. Paläontographica Ser A, **147**:169～216

Wellnhofer P, 1993. Das siesta Exemplar von *Archaeopteryx* aus den Solnhofener Schichten. Archaeopteryx, **11**:1～47

Xu X, Wang X, Wu X, 1999. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. Nature, **401**:262～266

Yoshitsugu K, Lü J, Dong Z *et al.*, 1999. Herbivorous diet in an ornithomimid dinosaur. Nature, **402**:480～481

Zhou Z, 1995. Is *Mononykus* a bird? The Auk, **112**:958～963

Zhou Z, Jin F, Zhang J, 1992. Preliminary report on a Mesozoic bird from Liaoning, China. Chinese Sci Bull,

37(16): 1363～1368

Zhou Z H(周忠和), Hou L H(侯连海), 1998. *Confuciusornis* and the early evolution of birds. Vert PalAsiat(古脊椎动物学报), **36**(2): 136～146

Zhou Z, Martin L D, 1999. Feathered dinosaur or bird?—a new look at the hand of *Archaeopteryx*. Smithson Contrib Paleobiol, **89**: 289～293

Explanations of plates

Plate I

Holotype of *Caudipteryx dongi* sp. nov. (IVPP V 12344), ×0.26

Plate II

Forelimbs of *Caudipteryx dongi* sp. nov. (IVPP V 12344), ×1

Plate III

Ilia of *Caudipteryx dongi* sp. nov. (IVPP V 12344), top, left side in medial view, overlapped by caudal vertebrae; bottom, right side in lateral view, ×1

Plate IV

Hindlinbs of *Caudipteryx dongi* sp. nov. (IVPP V 12344), left, right side in postero-medial view, showing reversed hallux; right, left side in lateral view, ×1

Plate V

Primary feathers of *Caudipteryx dongi* sp. nov. (IVPP V 12344), ×2.5



